Brachiopods from the uppermost Lower Ordovician of Peru and their palaeogeographical significance

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The studied brachiopod assemblages from the uppermost Lower Ordovician beds of Peru are of very low diversity and are among the northernmost known strata of that age in South America. They have been collected at the Carcel Puncco canyon of the Inambari River, near San Gabán in the easternmost Eastern Cordillera. Of the six species described, *Euorthisina orthiformis* and *Paralenorthis immitatrix* were already known from the Bolivian outcrops of the same Andean Eastern Cordillera; two species are new: *Ahtiella zarelae* Villas sp. nov. and *Paralenorthis carlottoi* Villas sp. nov. The new species of *Ahtiella*, of late Floian age, represent the oldest record of the genus characteristic of Celtic assemblages. During the early Mid Ordovician the genus migrated eastward from this region into the north margin of proto-Avalonia and after that, in Llanvirn times, into Baltica. During the early Llanvirn *Ahtiella* also migrated westward reaching the Precordillera Argentina region. Brachiopod faunal affinities suggest that there was a closer proximity of Avalonia with the Central Andean Basin, in similar temperate latitudes, than with the Southwestern European Platform, placed in very high latitude. *Paralenorthis* does not give any palaeogeographical signal, since it is known from all latitudes and palaeocontinents. Nevertheless, the occurrence of *Euorthisina* reinforces the Gondwanan signature of the region, since this genus spread during the Arenig throughout the middle latitude belt at the Gondwana margins, although it also colonised sub-polar latitudes, coinciding with the Llanvirn transgression over North Gondwana.

Key words: Brachiopoda, palaeogeography, Ordovician, Arenig, Gondwana, Celtic Province.

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Introduction

Lower Ordovician brachiopods of South America are well known from Bolivia (Havlíček and Branisa 1980) and Argentina (Benedetto 2003b and references therein) but very poorly from the northern Ordovician outcrops of the Andean Eastern Cordillera, where the Peruvian successions belong (Fig. 1). The occurrence of low diversity brachiopod associations from the uppermost Lower Ordovician (middle Arenig) of Peru extends the distribution of those organisms through the western margin of Gondwana and allows a better understanding of their relationships with those in the peri-Gondwanan part of Avalonia.

Brachiopods are of great value in reconstructing the Ordovician palaeogeographical configuration of the Proto-Andean margin of Gondwana; they are among the main tools used in discussion of the origin of the Argentine Precordillera terrane (Benedetto 1998a). Nevertheless, their knowledge in South America is greatly unbalanced, with important studies in the Lower Ordovician of the Argentine Precordillera and Famatina (Benedetto 2003b and references therein) but few on those regions with clearest Gondwanan connections, mainly Bolivia (Havlíček and Branisa 1980) and northwest Argentina (Benedetto 1998b; Benedetto and Carrasco, 2002; Harper et al. 2004; Villas and Herrera 2004). Improving the knowledge on the Ordovician brachiopods from the Central Andean Basin will help in understanding the relationships between the autochthonous Gondwanan regions and those with a disputed allochthonous origin. Moreover, since few data on Early Ordovician brachiopods are known in South America northward of Bolivia (Harrington and Kay 1951), difficulties exist in understanding the biogeographic relationships between the western Gondwana South American margin, the north Gondwana Afro-South European margin and the intermediate Avalonian margin. With the present paper we hope to shed a new light on those biogeographic relationships.

Institutional abbreviations.—MGM, Museo Geominero in Madrid, Spain (numbers MGM 5888X–5997X); INGEMMET Peruvian Geological Survey (palaeontological collection), Lima, Peru.

Geographical and geological setting

The fossiliferous locality is within the Carcel Puncco Canyon of the Inambari River, about 20 km northwest of the town of San Gabán, in the easternmost Eastern Cordillera of

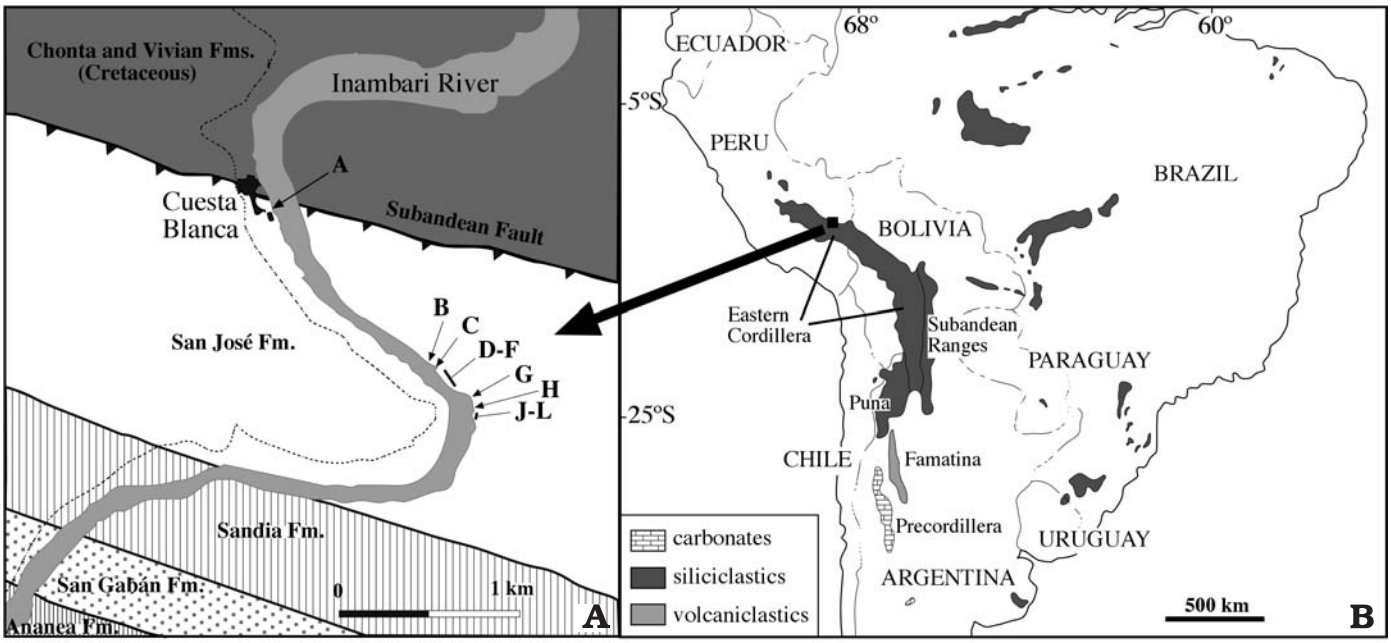


Fig. 1. Location of the studied fossiliferous localites A–L. **A**. Geological map of the Carcel Puncco Canyon, with the lithostratigraphic boundaries modified from Laubacher (1977) and Palacios et al. (1996, Masuco Quadrangle). **B**. Map of the main Lower Palaeozoic outcrops of southern South America (after Astini 1995).

Peru. The discovery of Ordovician fossils from this section was noted by Dávila and Ponce de León (1973), who recorded some brachiopods (*Orthis* sp.), trilobites and graptolites from Ordovician rocks, assigned to a late Arenig or Llanvirn age. Slightly later, Laubacher (1974, 1977) established more accurately the stratigraphy and age of the Ordovician succession, describing, in the Carcel Puncco section, a lower shale unit about 800 m thick, the San José Formation (Arenig to lower Caradoc), and an upper sandy and quartzitic unit about 500 m thick, the Sandia Formation (middle to upper Caradoc). The base of the first formation is truncated by the Quincemil Fault, connecting the Ordovician outcrops of the Eastern Cordillera that overthrust the Cretaceous limestones and sandstones of the Subandean Zone. The Sandia Formation is overlain by glaciomarine shales and quartzites correlated with the Hirnantian? to Lower Silurian Zapla–Cancañiri Formation (locally known as San Gabán Formation: Palacios et al. 1996; Cerpa et al. 2000; Díaz-Martínez 2005), which is overlain by a monotonous sequence of dark argillaceous shales known as the Ananea Formation (Middle Silurian to Devonian).

Among the fossils from the San José Formation, Laubacher (1974, 1977) listed some Arenig to Llanvirn trilobites, molluscs, graptolites and echinoderms, together with indeterminate orthid brachiopods. A more complete account of the Ordovician fossils from the Carcel Puncco Canyon was provided by Palacios et al. (1996), who listed and figured the brachiopods *Valcourea* cf. *strophomenoides*, *Paralenorthis* cf. *riojanus*, *Phragmorthis* cf. *buttsi*, *Orthambonites* sp., *Cyrtonotella* sp., and *Dinorthis* sp. from the San José Formation in association with some trilobites and ostracods, together suggesting a Llanvirn age. Most of those brachiopods must correspond with the forms identified herein, but neither with the published figures in the Palacios et al. (1996) paper nor with the poorly preserved original specimens stored in the collections of INGEMMET is possible to construct a precise synonymy list. A recent biostratigraphical reappraisal of the section led to the discovery of the first undisputable Arenig fossils, including conodonts (Sarmiento et al. 2001) as well as diverse trilobites, gastropods, rostroconchs, bivalves, echinoderms, graptolites, and brachiopods. Preliminary conclusions on the brachiopods described herein were presented by Gutiérrez-Marco et al. (2004) and Villas et al. (2004, 2006).

The studied brachiopods were collected by the first author in 2002 and 2004, and are from twelve fossiliferous horizons, A to L, cropping out at the eastern and western banks of the Inambari River near the Cuesta Blanca village (Figs. 1 and 2). All of them are within a 200 m thick interval in the lower half of the San José Formation, which is here of clear Arenig age according to the record of Early Ordovician conodonts (Sarmiento et al. 2001) and also by its position ranging well below the FAD of some Middle Ordovician graptolites such as *Aulograptus*, pendent *Didymograptus* or primitive biserial forms. These graptolites appear first 30–60 m above the highest studied horizons with the brachiopods of the San José Formation. The single record so far of conodonts is from a thin bioclastic limestone, about 100 m above the local base of the San José Formation, where several taxa characterizing the upper part of the *Oepikodus evae* Biozone have been recognized (Sarmiento et al. 2001; Gutiérrez-Marco et al. 2004). Therefore, it can be correlated with the

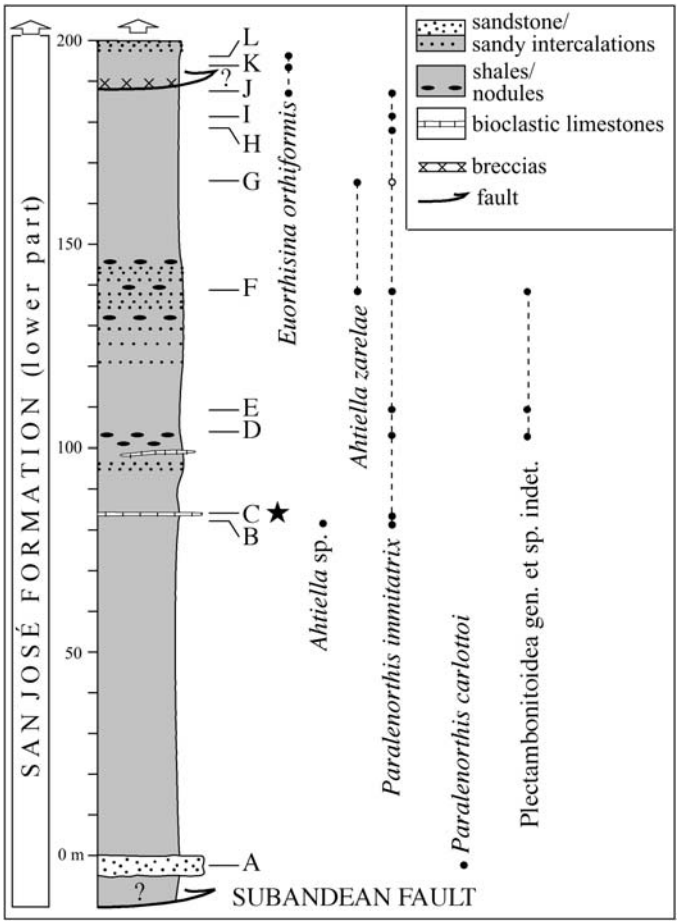


Fig. 2. Stratigraphic scheme of the lower part of the San José Formation at the Carcel Puncco Canyon (Inambari River), showing the position of the fossiliferous horizons yielding the studied brachiopods. The open circle indicates probable occurrence. Black star indicates the occurrence of late Floian (Early Ordovician) conodonts belonging to the upper part of the *Oepikodus evae* Biozone (Sarmiento et al. 2001; Gutiérrez-Marco et al. 2004).

uppermost Lower Ordovician Series (upper Floian Stage according to the new global chronostratigraphic terminology), as well as with the Whitlandian (middle Arenig Series) of the British-Avalonian regional scheme.

The examined strata generally strike at 110–125°N and dip at 70–80°S. Shales and dark mudstones are the main lithologies of the San José Formation, whose lower half in the Carcel Puncco section includes some local intercalations of quartzites (near the base) and thin lenticular bioclastic limestones towards its lower part. Other noticeable beds are some levels rich in siliceous and carbonatic nodules, as well as rarer thin sandy intercalations (usually millimetric, rarely centimetric). Some basic intrusive rocks are also represented as tabular oblique beds, about 185 m above the basal quartzite.

The studied brachiopods occur mostly as internal and external moulds preserved in shales and sandstones with some to severe compactional deformation, besides full relief moulds delicately preserved in nodules, or in brachiopod-trilobite coquinas within the rare limestone beds.

Besides the Carcel Puncco section in the Subandean area, the only other area with Arenig fossils from the lower part of the San José Formation, yielding a partly coeval and rather similar brachiopod fauna, is along the creeks on the right margin of the Apurímac River in the western flank of the Eastern Cordillera, which is here known as the Vilcabamba Cordillera. From this region, Aldana (in Monge et al. 1998) listed and partly figured: *Orthis* cf. *swanensis*, *Dinorthis* sp., *Glyptorthis* sp., *Multicostella* cf. *semisulcata*, *Harknessella* sp. and *Sowerbyella* sp., of possible Arenig–Llanvirn age. This assemblage has not been revised and lacks the adequate biostratigraphical control; a quick perusal of several of the original fossils collected by Monge et al. (1998) stored in the Geological Museum of the INGEMMET in Lima, suggests a great taxonomic and biostratigraphical significance.

Systematic palaeontology

(by Enrique Villas)

Order Strophomenida Öpik, 1934

Superfamily Plectambonitoidea Jones, 1928

Plectambonitoidea gen. and sp. indet.

Fig. 3C–F.

Material.—Internal and external mould of one ventral valve (MGM 5967), internal moulds of three ventral valves (MGM 5968X, 5970X, 5971X) and external moulds of two shells with conjoined valves (MGM 5969X, 5972X) from Carcel Puncco section; horizons D, E, and F of the San José Formation.

Description.—Shell convexoplane to convexoconcave, up to 9 mm long, transverselly elongate, 52–58% as long as wide, auriculate, with slightly invaginated anterior margin. Multicostellate to slightly parvicostellate, with accentuated ribs only in central part, 10 ribs per 2 mm counted five mm anteromedianly from umbo; strong and irregular growth striae accumulated on margin of shell; subtle impersistent rugae on posterolateral areas. Ventral valve plane to gently concave, except in the lateral extremities which are almost planar, with narrow and low median fold. Ventral interarea catacline, flat, 13–14% as long as valve, transversally striated, with apically perforated pseudodeltidium occupying delthyrium posterior half; delthyrium anterior half filled by cardinal process. Dorsal valve convex, with maximum depth posteriorly, subplanar lateral extremities and narrow sulcus. Dorsal interarea apsacline, flat, shorter than ventral interarea, with wide chilidium totally covering notothyrium and welded to possibly trifid cardinal process.

Ventral interior with strong teeth and conspicuous crural fossettes, very short dental plates converging onto valve floor and with bases diverging anteriorly; muscle field short, 30% as long as valve, 18–25% as wide as valve, bilobed, with diductor scars not enclosing anteriorly to adductor scars.

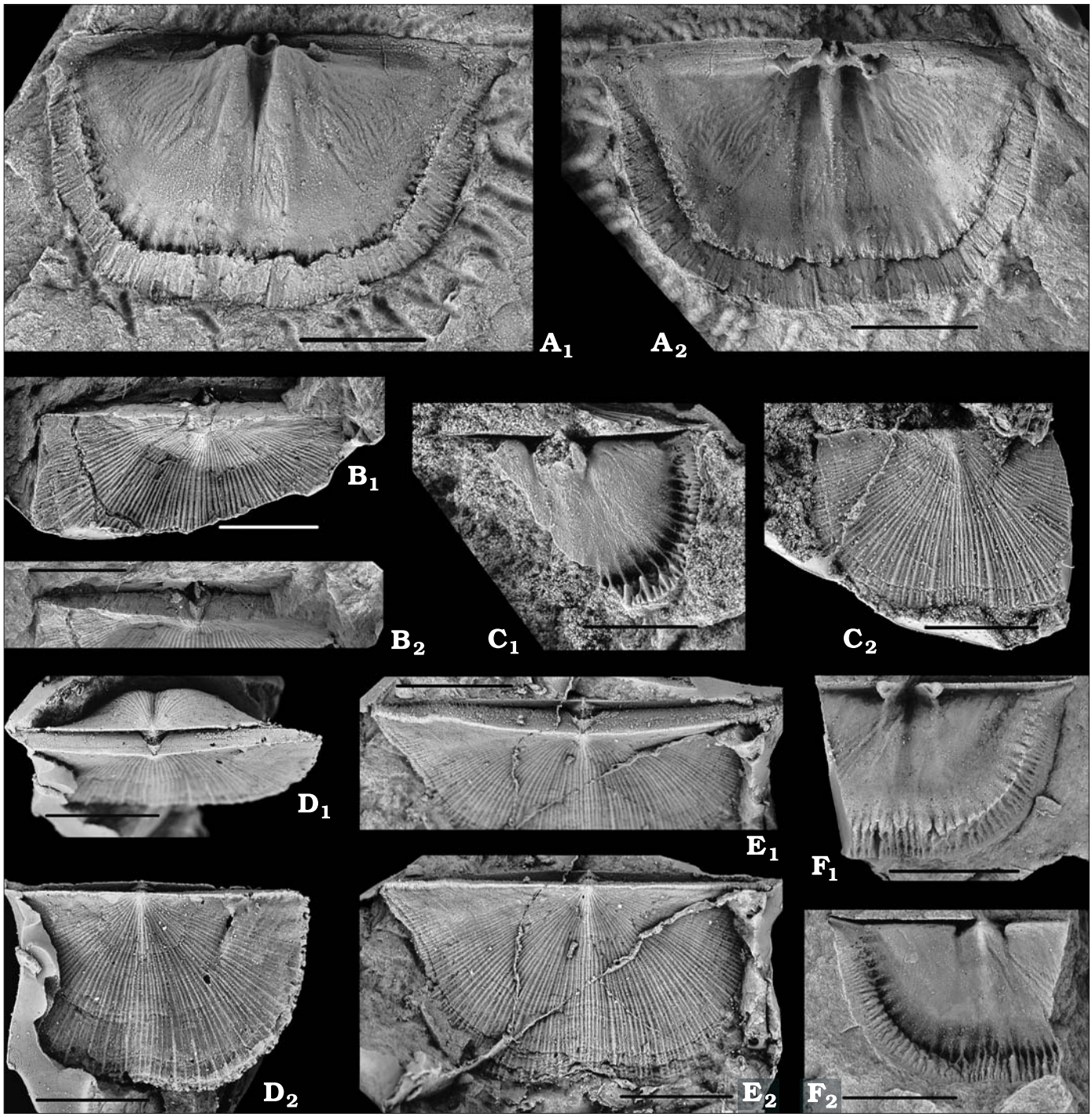


Fig. 3. Taffiid brachiopod *Ahtiella* sp. **A**. MGM 5965X, internal mould (A_1) and latex cast of interior (A_2) of dorsal valve. **B**. MGM 5966X, latex cast of exterior in ventral view (B_1) and postero-ventral view (B_2) of shell with conjoined valves . **C**–**F**. Plectambonitoidea gen. et sp. indet. **C**. MGM 5967X, internal mould (C_1) and latex cast of exterior (C_2) of ventral valve. **D**. MGM 5969X, latex cast of exterior in postero-ventral view (D_1) and ventral view (D_2) of shell with conjoined valves. **E**. MGM 5972X, latex cast of exterior in postero-ventral view (E_1) and ventral view (E_2) of shell with conjoined valves. **F**. MGM 5968X, latex cast of interior (F_1) and internal mould (F_2) of ventral valve. Scale bars 5 mm.

Very strong platform, 5–7 mm long, subtending angle of about 110° with underlying marginal area, but not related to any kind of geniculation of valve exterior. Vascula genitalia digitated very close to their origin at dental plate bases. Vascula terminalia strongly impressed on margin of platform and on valve margins.

Discussion.—It is not possible to precisely determine this plectambonitoid without knowing its dorsal interior, on which all the diagnostic characters for family and subfamily classification are based (Cocks and Rong 1989). An apparently trifid cardinal process, welded to a well developed chilidium, can be observed in the collected shells exteriors,

but it is not possible to ascertain if it is undercut or not. With only this information on their dorsal interior these shells can only be discriminated from the bimuriids, plectambonitids and taffiids, with simple cardinal processes, but could be assigned to any of the other seven families recognised within the superfamily (Cocks and Rong 1989). The resupinate profile of the studied shells, although not very common in any of these seven families, is not enough to discriminate among them.

Family Taffiidae Schuchert and Cooper, 1931

Subfamily Ahtiellinae Öpik, 1933

Genus *Ahtiella* Öpik, 1932

Type species: *Ahtiella lirata* Öpik, 1932; Darriwilian (Middle Ordovician), Tsitri, Estonia.

Ahtiella zarelae Villas sp. nov.

Fig. 4.

Derivation of the name: After Dr. Zarela A. Herrera, for her studies on South American Ordovician brachiopods.

Types: Holotype MGM 5935X. External mould of ventral valve.

Type locality: Carcel Puncco section, Inambari River, Cuesta Blanca village, 20 km NW of San Gabán, Eastern Cordillera, Peru.

Type horizon: Horizon G of the San José Formation, upper Floian Stage, uppermost Lower Ordovician Series.

Material.—Nearly a hundred internal or external moulds of ventral and dorsal valves, including numbers MGM 5925X–5964X, from the horizons F and G of the San José Formation.

Diagnosis.—*Ahtiella* with rectangular to slightly alate cardinal angles, pronounced carinate ventral fold and dorsal sulcus, fine ramicostellate ribbing and weak corrugation.

Description.—Shell resupinate, up to 15 mm wide, with maximum width at hinge line, rectangular to acute cardinal angles, some slightly alate; anterior commissure plicate. Ventral valve concave and slightly geniculate in adult stages, with high angulose and narrow, carinate, median fold, mean length relative to width of 0.54 (number [n] = 33, variance [v] = 0.004), up to 37% as deep as long, with trail slightly differentiated at anteriormedian region from disc 4.5–7 mm long; ventral interarea flat, catacline to steeply apsacline, about 15% as long as valve, with apical pseudodeltidium. Dorsal valve strongly convex in adult stages, with deep median sulcus, having v-shaped cross-section, mean length relative to width of 0.60 (n = 21, v = 0.003), up to 33% as deep as long, with anacline to orthocline dorsal interarea, 3–7% as long as valve, with poorly preserved chilidium. Radial ornamentation uniformly ramicostellate, with 10–12 ribs, very rarely 13, per 2 mm counted 5 m anterolaterally from umbo, intersected by filae, with counts of about 20 per mm. Occassionally with 2–3 rugae on posterior margins, strongly oblique to subparallel to hinge line.

Ventral interior with triangular teeth, supported by short dental plates, continuous anteriorly with very low lateral muscle bounding ridges; muscle field subpentagonal, with mean length relative to valve length of 0.25 (n =17, v = 0.002), mean width relative to valve width of 0.18 (n = 17, v = 0.002), adductor scar as wide as each diductor scar and not enclosed anteriorly by them. Ribbing strongly impressed on interior of trail, as well as on margins of disc of large valves, with ridges corresponding to external intercoastal furrows accentuated by pustules. Conspicuous narrow and deep sulcus-like impression of external median fold.

Dorsal interior with simple cardinal process, short notothyrial platform continuous anteriorly with septum-like impression of external median sulcus; median sulcus is highest at its anterior end, at margin of platform, where it is strenghtened by elongated pustules. Socket ridges small bounding triangular sockets; quadripartite muscle field only poorly impressed in largest valves. Subperipheral rim low, emerging from cardinal angles, bounding a platform 5–7 mm long. Ribbing also strongly impressed on internal margin of dorsal valves, accentuated by pustules.

Discussion.—This plectambonitoidean can clearly be ascribed to *Ahtiella* based on its convexo-concave profile, simple geniculation, impersistent rugae and dorsal median septum. It differs from the congeneric Baltic species *A. arenaria* Öpik, 1933, *A. baltica* Öpik, 1932 and *A. lirata* Öpik, 1932 by its well developed ventral fold and dorsal sulcus, and from *A. jaanussoni* Hessland, 1949 for its much less developed rugae. It coincides with the Welsh *A. concava* Bates, 1968 in outline and the prominent fold and sulcus but lacks its typical strong lateral ridges radiating from posterior dorsal muscle scars. It differs from *A. quadrata*, also from Wales and the oldest known species of the genus, for the parvicostellate and much thicker ribbing of the latter, with only 6 ribs per 2 mm. The Peruvian species can be distinguished from *A. argentina* Benedetto and Herrera, 1986, from the Argentine Precordillera, by the strongly mucronate outline, not so accentuated fold and sulcus, more prominent rugae and parvicostellate ribbing of the Argentine species. It compares with the North American *A. paucirugosa* Neuman, 1977 in the weak rugosity and pronounced fold and sulcus, but differs from it in its ramicostellate ornamentation, in contrast to the parvicostellae in the North American species, and its much shorter ventral muscle field.

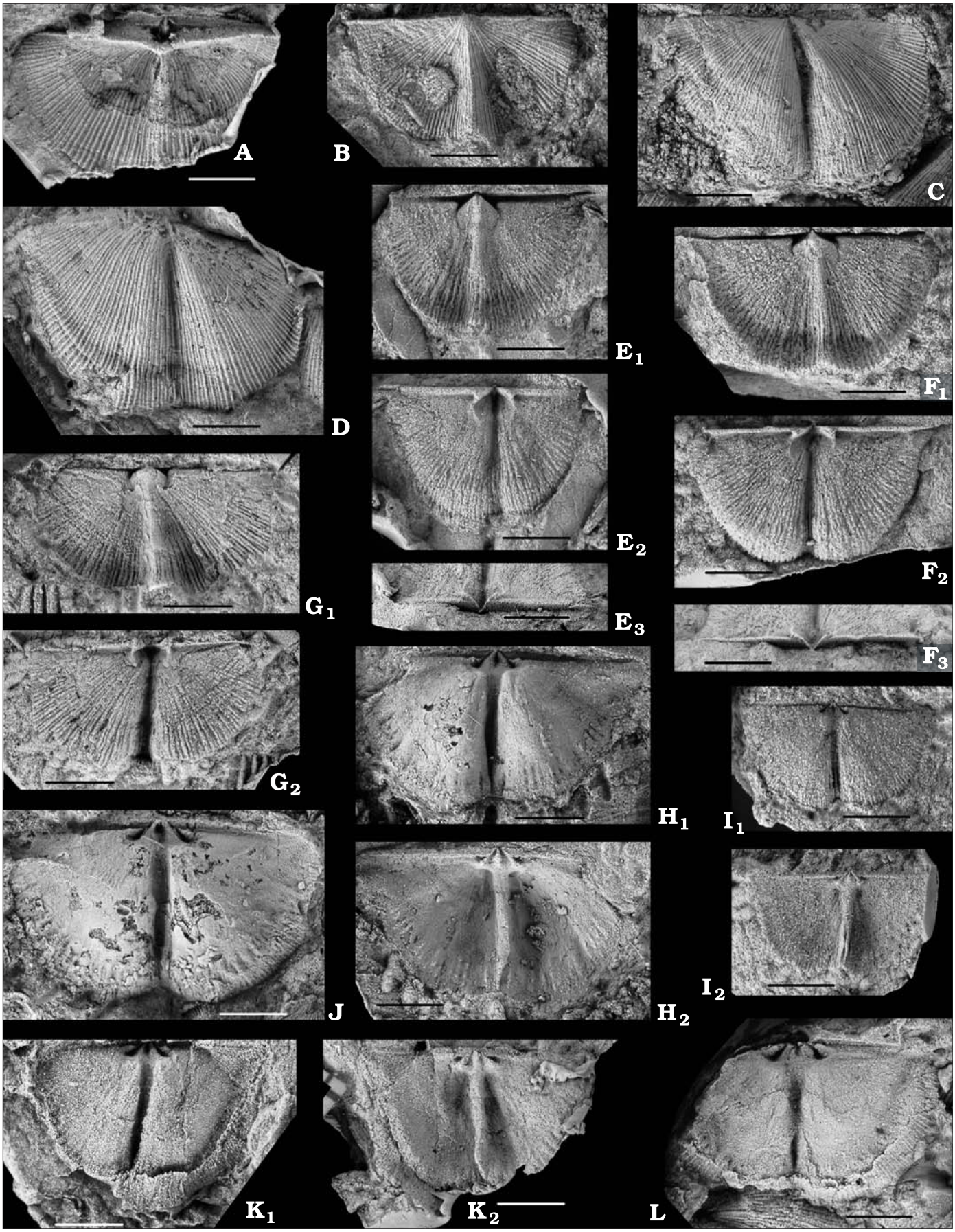
The new species is close to *Ahtiella* sp. (Benedetto 2003b: 210), from the Arenig Suri Formation of Famatina (Argentina), in its ventral and dorsal interiors, as well as in its uniformly ramicostellate ornamentation, which is only slightly finer in the Peruvian shells. Nevertheless, these can be discriminated from the Argentine *Ahtiella* sp. for their much more pronounced ventral fold and dorsal sulcus.

Stratigraphic and geographic range.—It is only known from its type locality, at the Carcel Puncco section, in the horizons F and G of the San José Formation.

Ahtiella sp.

Fig. 3A, B.

Material.—Internal mould of a dorsal valve and external mould of the dorso-posterior part of a shell with conjoined


A
B
C
D
E1
F1
E2
F2
E3
F3
G1
G2
H1
I1
J
H2
I2
K1
K2
L

valves from Carcel Puncco section; horizon B of the San José Formation.

Description.—Shell resupinate, up to 19 mm wide, with maximum width at hinge line, acute, slightly alate cardinal angles; anterior commissure rectimarginate to very slightly plicate. Ventral valve concave, with very low and narrow median fold; ventral interarea flat, catacline, with arched pseudodeltidium half as long as interarea. Dorsal valve strongly convex, with maximum convexity at posterior half and narrow and shallow median sulcus impressed on anterior margin of valve interior; 56% as long as wide and about 30% as deep as long, with orthocline to apsacline dorsal interarea, 8% as long as valve, without chilidium. Radial ornamentation uniformly ramicostellate, with ribs rounded in cross section, numbering 14 per 2 mm at 5 m anteromedially from umbo, intersected by filae. With a few slender rugae on posterior margins, strongly oblique to hinge line.

Ventral interior unknown. Dorsal interior with cardinal process simple, ridge-like, with ovoid base, and as long as notothyrial platform; notothyrial platform is short and thick, anteriorly excavated by posterior adductor scars, continuous anteriorly with strong median septum; median septum very thick and high between posterior adductor scars, narrowing and lowering forward to become a slender ridge at its anterior end and fade slightly beyond mid length of valve. Socket plates perpendicular to valve floor, strongly divergent anteriorly, bounding triangular sockets excavated on thick secondary shell deposits and partially under dorsal interarea, and halved by tiny bulbs welded to their posterior walls. Quadripartite muscle with trapezoidal posterior adductor scars, shorter than bilobed anterior adductor scars. Vascula genitalia strongly impressed on posteromedian part of valve, without reaching platform edge, as well as vascula myaria made up by four trunks arising from every lobe of anterior adductor scars, by two sub-median trunks subparallel and by two lateral trunks diverging anteriorly. Vascula media much narrower, running pararell to each other, separated by anterior end of median septum. Platform well developed, 83% as long as valve, with pustulose, anteriorly-excavated edges, difuminating close to cardinal angles. Ribbing strongly impressed on internal margin of dorsal valves.

Discussion.—The resupinate profile and simple cardinal process of this plectambonitoid are diagnostic of the subfamily Ahtiellinae. Within it, the presence or absence of a dorsal median septum have been considered an important character to differentiate its known genera (Cocks and Rong 1989). The median raised area of the studied dorsal valve can be considered a median septum since, although with a very slender anterior end, extends beyond the anterior margin of the muscle field and thus can be discriminated from a simple myophore. This allows the inclusion of these shells within *Ahtiella*. The dorsal median septum is very prominent in most of the known species of this genus and usually extends forward until the platform edge. Nevertheless, occasionally it fades forward as in *Ahtiella concava* where the septum only extends to "almost half the length of the valve" (Bates 1968: 168).

Thus, the relatively short dorsal median septum of this valve allows a ready discrimination from those *Ahtiella* species with known dorsal interiors and a long median septum as *A. argentina* Benedetto and Herrera, 1986, *A. jaanusoni* Hessland, 1949, *A. lirata* Öpik, 1932, *A. paucirugosa* Neuman, 1977, *A. quadrata* Bates, 1968, *Ahtiella* sp. (Benedetto 2003b: 210) and *A. zarelae* Villas, sp. nov. described above. It differs also from *A. concava* since, in spite of its relatively short dorsal median septum, this thickens and swollen in its anterior half (Bates 1968: 168). Because its uniformly ramicostellate ornamentation it can also be discriminated from *A. argentina* and *Ahtiella* sp. nov. (Benedetto 2003b: 201) that are parvicostellate. The weak rugosity of the Peruvian *Ahtiella* allows distinguishing it from the Baltic species, ascribed to *Ahtiella*, in spite of not knowing their dorsal interiors, *A. arenaria* Öpik, 1933, *A. baltica* Öpik, 1932, *A. dalecarlica* Hessland, 1949, *A. jentschi* (Gagel, 1890), *A. oelandica* Hessland, 1949 and *A. plana* Hessland, 1949, all of them with prominent rugae.

Only two specimens have been recorded of this *Ahtiella*, and its ventral interior is not yet known. Although its delicately preserved dorsal interior and a well known shell exterior allow a ready discrimination from all the described species of the genus, it seems advisable to await to the finding of new material before proposing formally a new species name.

Order Orthida Schuchert and Cooper, 1932

Suborder Orthidina Schuchert and Cooper, 1932

Superfamily Orthoidea Woodward, 1852

Family Orthidae Woodward, 1852

Genus *Paralenorthis* Havlíček and Branisa, 1980

Type species: *Paralenorthis immitatrix* Havlíček and Branisa, 1980; Floian (Lower Ordovician), San Lucas, Bolivia.

Paralenorthis immitatrix Havlíček and Branisa, 1980

Fig. 5.

1980 *Paralenorthis immitatrix* sp. nov.; Havlíček and Branisa 1980: 16, pl. 1: 1–9.

← Fig. 4. Taffiid brachiopod *Ahtiella zarelae* Villas, sp. nov. **A**. MGM 5943X, latex cast of exterior of a shell with conjoined valves in ventral view. **B**. MGM 5935X, latex cast of ventral exterior, holotype. **C**. MGM 5942X, latex cast of dorsal exterior. **D**. MGM 5944X, latex cast of dorsal exterior. **E**. MGM 5931X, internal mould (E_1) and latex cast of ventral interior in dorsal view (E_2) and postero-dorsal view (E_3) of ventral valve. **F**. MGM 5926X, internal mould (F_1) and latex cast of ventral interior in dorsal view (F_2) and postero-dorsal view (F_3) of ventral valve. **G**. MGM 5925X, internal mould (G_1) and latex cast of interior (G_2) of ventral valve. **H**. MGM 5945X-2, internal mould (H_1) and latex cast of interior (H_2) of dorsal valve. **I**. MGM 5929X, internal mould (I_1) and latex cast of interior (I_2) of dorsal valve. **J**. MGM 5945X-1, internal mould of dorsal valve. **K**. MGM 5930X-1, internal mould (K_1) and latex cast of interior (K_2) of dorsal valve. **L**. MGM 5946X-2, internal mould of dorsal valve. Scale bars 3 mm.

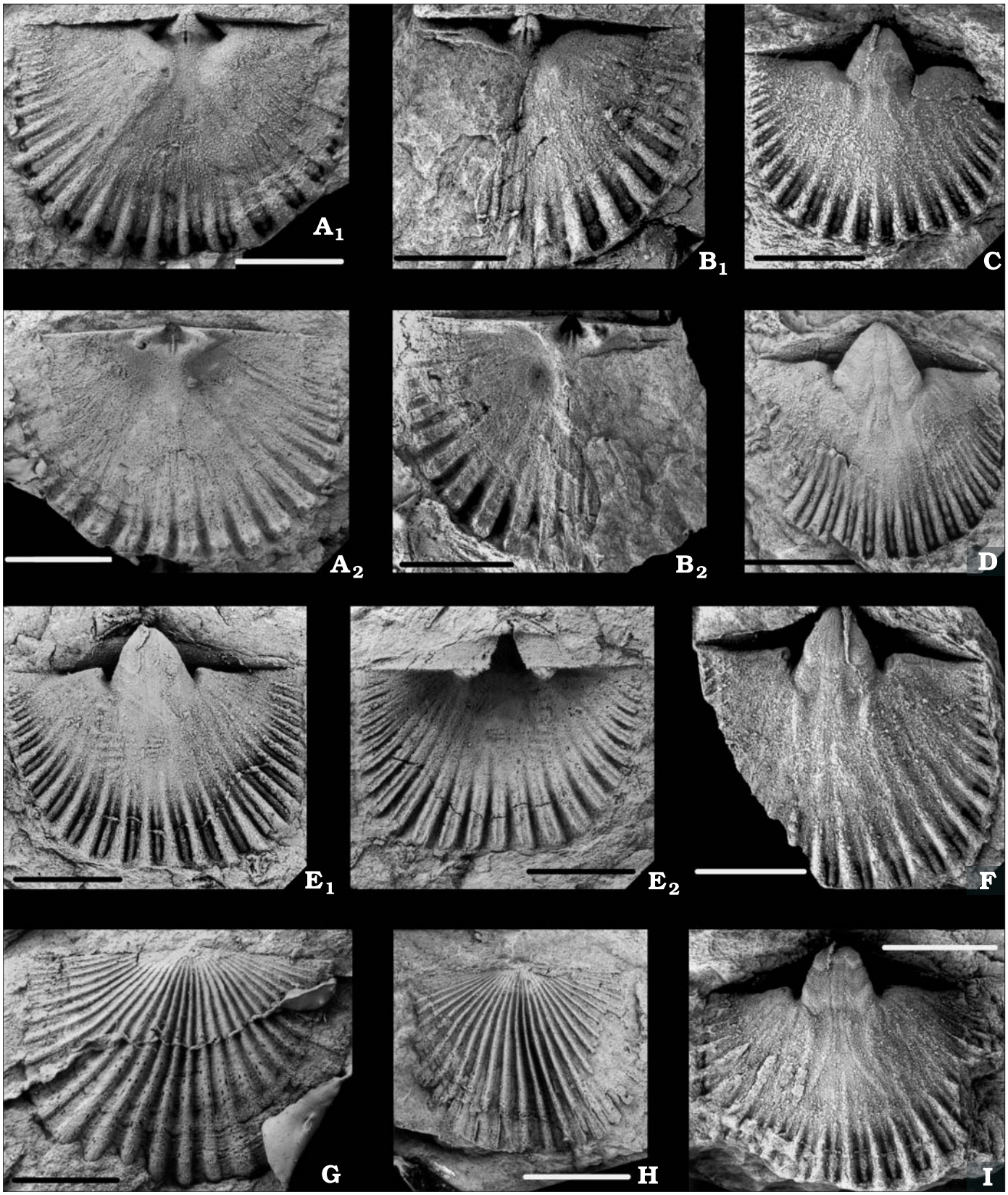


Fig. 5. Orthid brachiopod *Paralenorthis immitatrix* Havlíček and Branisa, 1980. **A**. MGM 5987X-2 internal mould (A_1) and latex cast of interior (A_2) of dorsal valve. **B**. MGM 5989X, internal mould (B_1) and latex cast of interior (B_2) of dorsal valve. **C**. MGM 5991X, internal mould of ventral valve. **D**. MGM 5988X, internal mould of ventral valve. **E**. MGM 5987X-1, internal mould (E_1) and latex cast of interior (E_2) of ventral valve. **F**. MGM 5992X, internal mould of ventral valve. **G**. MGM 5987X-2, latex cast of exterior of dorsal valve. **H**. MGM 5990X, latex cast of exterior of dorsal valve. **I**. MGM 5986X, internal mould of ventral valve. Scale bars 5 mm.

Material.—Six ventral valves and seven dorsal valves preserved as internal and external moulds with collection numbers MGM 5985X–5996X.

Distribution.—Carcel Puncco section; horizons B to F and H to J of the San José Formation.

Description.—Shell ventribiconvex, of subquadrate outline, 78–95% as long as wide, with maximum width along hinge line, rectangular to slightly acute cardinal angles, and slightly sulcate anterior commisure. Ventral valve convex, weakly carinate, 14–23% as deep as long, with maximum depth at umbonal area; ventral interarea apsacline to orthocline, slightly curve, 12–15% as long as valve, with open delthyrium. Dorsal valve weakly convex, 74–88% as long as wide, about 5% as deep as long, slightly sulcate with up to 4 costae on sulcus. Dorsal interarea curve, steeply anacline to catacline, with length half of that of ventral valve and open notothyrium. Ornamentation costate, capillate and filate, with high, subangular costae, numbering 27 in adult ventral valves and 28 in dorsal valves; capillae developed on intercostal spaces and on top of ribs; two rows of narrowly oval and shallow holes, perpendicular to the shell surface or at low angles directly posteriorly, clearly observable on top of median ribs at anterior half of shell (see Fig. 5G).

Ventral interior with strong deltidiodont teeth, with marked crural fossettes, supported by short dental plates; bilobed muscle field, 31–38% as long as valve, 26–36% as wide as valve, diductor scars longer than adductor scars, not enclosing them anteriorly, adductor scar 20–32% as wide as muscle field . Two strong vascula media arise from anterior end of diductor scars and immediately diverge anteriorly; ribbing strongly impressed on internal valve margins of both valve interiors.

Dorsal interior with blade-like cardinal process, on short notothyrial platform, about 15% as long as valve, almost completely restricted to posteriorly sloping notothyrial cavity, which extends anteriorly as median ridge to bisect dorsal muscle field; muscle field about 33% as long as valve and 31–35% as wide as valve; with wide dental sockets excavated on secondary shell deposits, and blade-like brachiophores.

Discussion.—These shells are assigned to *Paralenorthis immitatrix* Havlíček and Branisa, 1980, based on their number of ribs, shell outline and cardinalia. The large number of ribs is one of the most typical features of this species, with about 26 in the Bolivian types (Havlíček and Branisa 1980) and up to 28 in the Peruvian specimens, herein studied. They also have a posteriorly sloping notothyrial platform and are similar in such a small detail as the short ridges bisecting posteriorly each dental socket. The ventral muscle field is rather variable, with a lateral enlargement in some specimens that makes each diductor scar almost double in width than adductor scar (Fig. 5D); other ventral valves display narrower muscle fields, with diductor scars of about the same width than adductor scar, as those described by Havlíček and Branisa (1980) from Bolivia.

The external holes of the studied shells (Fig. 5G) had not been observed previously either in its species or in its genus. But similar microstructures, interpreted as exopunctae (Williams 1974: 55; Jaanusson and Bassett 1933: 41), are known in the family Orthidae from two species of the genus *Sulevorthis* (Jaanusson and Bassett 1993): *S. lyckholmiensis* (Wysogórski, 1900) and *S. exopunctatus* (Williams, 1974), where they also can occur forming two rows on each costa as in the studied specimens of *P. immitatrix*. Probably these microstructures was also shared by other genera within the family Orthidae.

Paralenorthis carlottoi Villas sp. nov.

Fig. 6.

Derivation of the name: After Dr. Víctor Carlotto for his studies on the Peruvian Palaeozoic.

Holotype: MGM 5973X-1. External mould of ventral valve.

Type locality: Cuesta Blanca village, Inambari River, 20 Km NW of San Gabán, Eastern Cordillera, Peru.

Type horizon: Horizon A of the San José Formation, upper Floian Stage, uppermost Lower Ordovician Series.

Material.—About a hundred ventral and dorsal valves from the horizon A of the San José Formation, preserved as internal or external moulds, including numbers MGM 5973X–5984X.

Diagnosis.—*Paralenorthis* species with rectangular cardinal angles, costate and capillate, with 18–20 costae in adult dorsal valves, only two median costae occupying median sulcus, ventral muscle field 26–33% as long as valve, notothyrial platform restricted to notothyrial cavity and 14–22% as long as valve, blade-like divergent brachiophores and low median ridge.

Description.—Shell ventri-biconvex, up to 10 mm long, of semicircular outline, with maximun width on hinge line, rectangular cardinal angles and slightly sulcate anterior commissure. Ventral valve convex, 20–30% as deep as long, maximun depth at umbonal region, 71–98% as long as wide; ventral interarea curve, apsacline, 10–15% as long as valve, with open delthyrium. Dorsal valve weakly convex, 70–90% as long as wide; dorsal interarea curve, anacline, nearly as long as ventral interarea, with open notothyrium.

Radial ornamentation costate and capillate, with a single ventral valve showing ramification of one costae (see Fig. 6B); ribs counts of 17–21 in ventral valves and 18–20 in dorsal valves, with only the two dorsal median costae occupying median sulcus.

Ventral interior with apical collar, triangular teeth, short but high dental plates, triangular muscle field 26–33% as long as valve and 20–30% as wide as valve, with adductor scar 40–50% as wide as muscle field, and nearly as long as diductor scars, not enclosed anteriorly by these. Vascula media poorly impressed, divergent anteriorly.

Dorsal interior with blade-like cardinal process borne on long notothyrial platform restricted to notothyrial cavity, 14–22% as long as valve; blade-like divergent brachiophores, deep dental sockets excavated on thickening of valve floor,

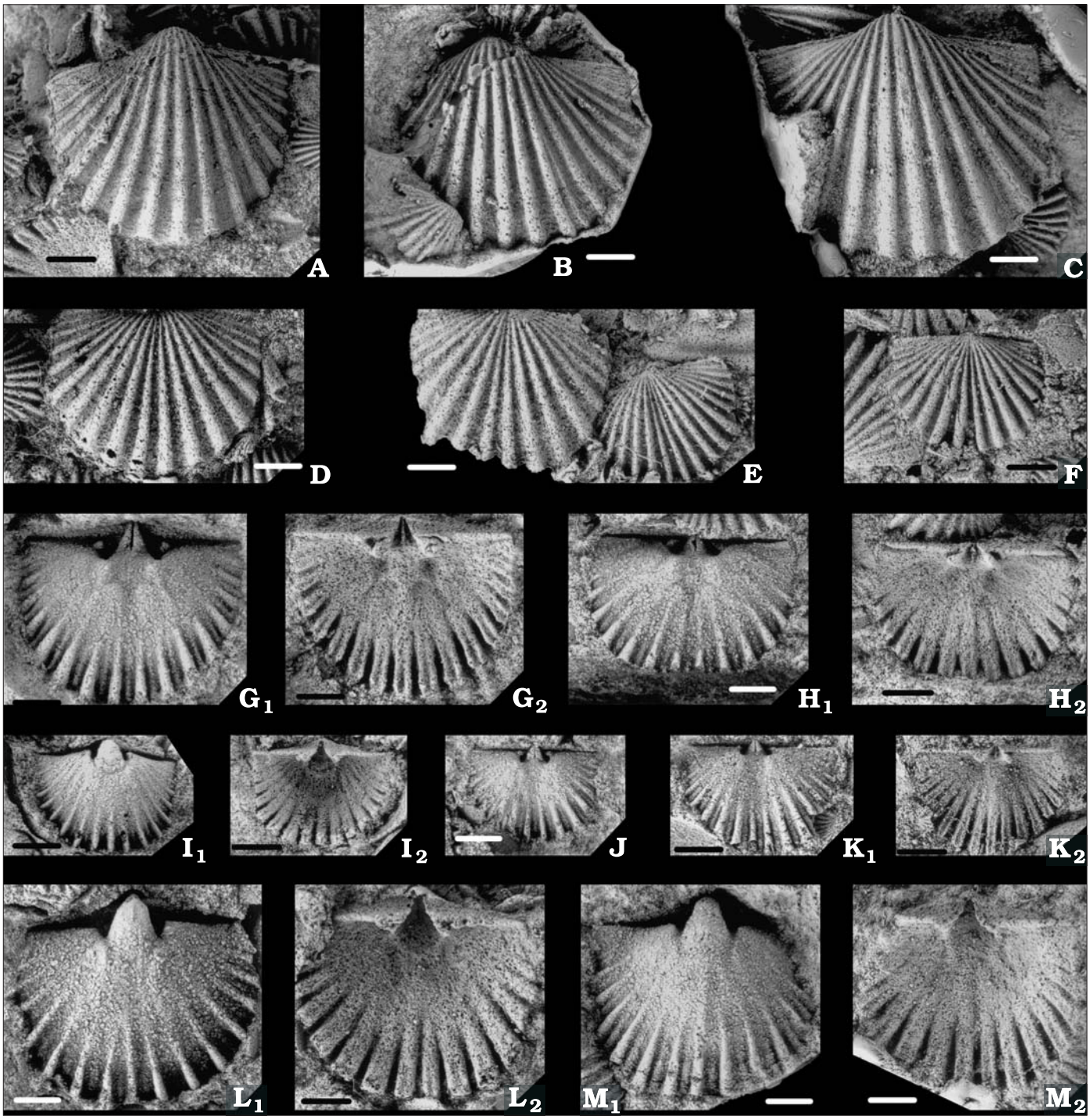


Fig. 6. Orthid brachiopod *Paralenorthis carlottoi* Villas, sp. nov. **A**. MGM 5973X-1, latex cast of exterior of ventral valve, holotype. **B**. MGM 5977X, latex cast of exterior of ventral valve. **C**. MGM 5975X, latex cast of exterior of ventral valve. **D**. MGM 5973X-6, latex cast of exterior of dorsal valve. **E**. MGM 5981X-2–3, latex casts of exteriors of two dorsal valves. **F**. MGM 5978X-2, latex cast of exterior of dorsal valve. **G**. MGM 5981X-1, internal mould (G_1) and latex cast of interior (G_2) of dorsal valve. **H**. MGM 5973X-4, internal mould (H_1) and latex cast of interior (H_2) of dorsal valve. **I**. MGM 5973X-2, internal mould (I_1) and latex cast of interior (I_2) of ventral valve. **J**. MGM 5973X-5a, internal mould of dorsal valve. **K**. MGM 5974X, internal mould (K_1) and latex cast of interior (K_2) of dorsal valve. **L**. MGM 5980X, internal mould (L_1) and latex cast of interior (L_2) of ventral valve. **M**. MGM 5979X, internal mould (M_1) and latex cast of interior (M_2) of ventral valve. Scale bars 2 mm.

wide and low median ridge, bisecting a quadripartite muscle field, about 50% as long as valve and 25–37% as wide as valve, with anterior adductor scars larger than posterior.

Internal margins of both valves crenulated with deep and narrow grooves, corresponding to crest of ribs, and wide eminences with shallow sulci on intercoastal spaces.

Discussion.—The divergent ventral vascula media, typical of *Paralenorthis* Havlíček and Branisa 1980, are poorly developed in a few of the studied valves (Fig. 6L), but their small size, besides the main external and internal features also points to an assignment to that genus, thoroughly revised by Jaanuson and Bassett (1993). These specimens can be discriminated from all the known species of *Paralenorthis* and thus the erection of a new species is proposed.

Paralenorthis carlottoi Villas sp. nov. displays a much lower number of ribs than *P. immitatrix*, the type species of the genus which also occur in the studied succession as well as in the Arenig of Bolivia (Havlíček and Branisa 1980). Its ornamentation is not distinguishable from that of the Argentine *P. altiplanicus* Benedetto, 1998, although its notothyrial cavity is much broader and longer: 14–22% as long as valve in *P. carlottoi* while 10–13% as long as valve in *P. altiplanicus* (Benedetto 1998b: 13). The new species is also close to the British *P. proava* (Salter, 1866) in shape, number and wave length of ribs, but it displays only two ribs on the dorsal sulcus while there are four ribs in *P. proava*; they also differ in the relative size of the dorsal median ridge and the length of the ventral muscle field that is shorter in *P. carlottoi*. This can be also distinguished from *P. parvicrassicostatus* (Cooper, 1956), which is close to *P. proava* by the non capillate external surface of *P. parvicrassicostatus* (see Williams 1974). The Baltoscandian *P. orbicularis* (Pander, 1830) displays a very variable radial ornament that is occasionally similar to that of the new species; nevertheless, its ventral interarea is longer and the ventral valve is less strongly convex than in *P. parvicrassicostatus*. The Peruvian form has an ornamentation very similar to the North American *P. buttsi* (Schuchert and Cooper, 1932) , but they differ in their brachiophore bases, strongly convergent towards the bottom of the notothyrial cavity in the latter, as well as in the median septum, higher and narrower in *P. buttsi*. The new species is also very close in its ornamentation to *Orthis serica* Martelli, 1901 from South China, assigned to *Paralenorthis* by Jaanusson and Basset (1993); nevertheless can be distinguished by its more prominent ventral umbo, better developed dorsal median sulcus and longer ventral muscle field than in *P. serica* (see Xu and Liu 1984: pl. 2: 15, 16, 19–29).

The lack of auriculation in the new species allows ready distinction from the British *P. alata* (J. de C. Sowerby, in Murchinson, 1839), the Argentine *P. riojanus* (Levy and Nullo, 1973) and *P. suriensis* Benedetto, 2003, as well as the North American *P. marshalli* (Wilson, 1926), *P.*? *minusculus* (Phleger, 1933) and *P.*? *angulata* (Cooper, 1956).

The semicircular outline of the Peruvian *Paralenorthis*, with its maximum width at the hinge line, allows discrimination from the Argentine *P. vulgaris* (Herrera and Benedetto, 1989) and the North American *P. robusta* (Neuman,1964), whose outline is rounded, cardinal angles obtuse and the maximum width occurs in front of the hinge line.

Stratigraphic and geographic range.—It is only known from its type locality and horizon, at the Cuesta Blanca village, Inambari River, 20 km NW of San Gabán, Eastern Cordillera, Peru., in the horizon A of the San José Formation, upper Floian Stage, uppermost Lower Ordovician Series.

Superfamily Plectorthoidea Schuchert and Cooper, 1931

Family Euorthisinidae Havlíček, 1977

Genus *Euorthisina* Havlíček, 1951

Type species: *Orthisina moesta* Barrande, 1879; Darriwilian (Middle Ordovician), Bohemia, Czech Republic.

Euorthisina orthiformis Havlíček and Branisa, 1980

Fig. 7.

1980 *Euorthisina orthiformis* sp. nov.; Havlíček and Branisa 1980: 27–28, pl. 4: 4, 9–12.

Material.—23 ventral valves and 19 dorsal valves preserved as internal and/or external moulds, with collection numbers MGM 5888X–5924X and 5997X, from Carcel Puncco section; horizons J, K and L in the of the San José Formation.

Description.—Shell up to 23 mm wide, equibiconvex, with transversally oval outline, maximum width at posterior third of shell, hinge line 77–97% as wide as valve, with rounded slightly obtuse cardinal angles and rectimarginate anterior commissure. Ventral valve gently and evenly convex, with very slightly developed umbo, 64–91% as long as wide, ventral interarea attitude and delthyrium not observable due to flattening. Dorsal valve gently and evenly convex, 62–87% as long as wide, with narrow sulcus in early growth stages; dorsal interarea attitude and notothyrium not seen due to flattening.

Radial ornament ramicostellate and filate, with very irregular branching, asymmetrical on both sides of valve; ribs triangular in cross-section, although rounded in flattened shells, especially on anterior and lateral margins of valve. Irregular ribbing with ventral median rib deviating from the median line in its forward growth; correspondingly, one of the two dorsal median ribs occupies the median line after early growth stages. With fine fila, numbering about 15 per mm, arranged in rugose irregular bands.

Ventral interior, with subvertical dental plates, continuous anteriorly with muscle bounding ridges, very slightly divergent anteriorly in early stages and then subparallel, extending anteriorly to 16–17% of valve length. Undifferentiated triangular muscle field.

Dorsal interior with brachiophore plates converging to form v-shaped septalium, 4–7% as long as valve, supported by median septum that extends anteriorly 14–21% of valve length. Muscle field not observed. Ribs and rugose bands well marked on interior of both ventral and dorsal valves.

Discussion.—In spite of the strong flattening of most of these *Euorthisina* shells, several peculiar features, diagnostic of the Bolivian species *Euorthisina orthiformis* Havlíček and Branisa, 1980, can be seen, such as the strong irregularity of its ramicostellate ornamentation and the triangular section of the ribs. The latter feature is most evident in the

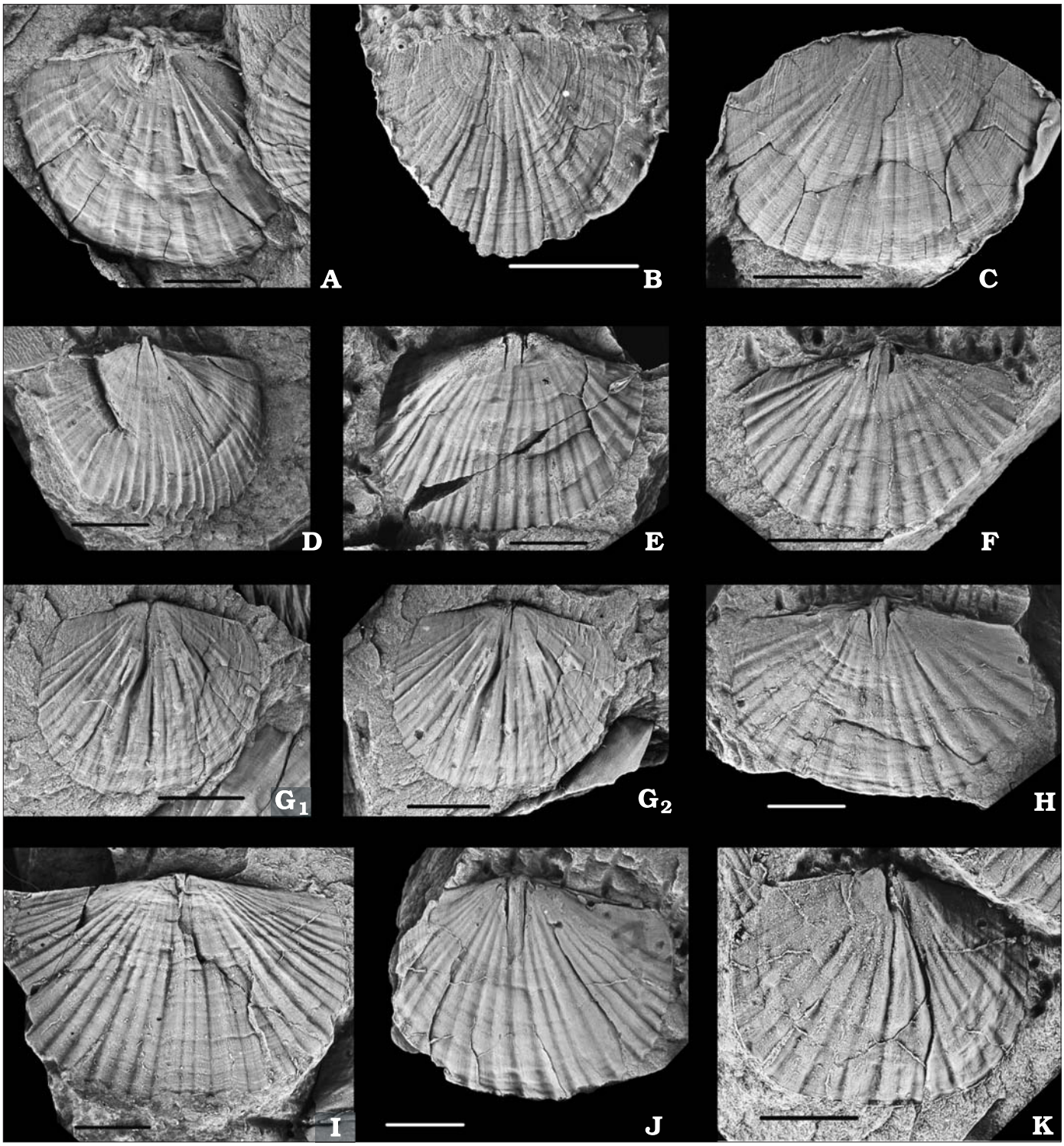


Fig. 7. Euorthisinid brachiopod *Euorthisina orthiformis* Havlíček and Branisa, 1980. **A**. MGM 5913-X3, latex cast of ventral exterior. **B**. MGM 5997X, latex cast of dorsal exterior. **C**. MGM 5915X, latex cast of dorsal exterior. **D**. MGM 5898X, internal mould of ventral valve. **E**. MGM 5897X, internal mould of ventral valve. **F**. MGM 5902X, internal mould of ventral valve. **G**. MGM 5913X-2, latex cast of exterior (G_1) and internal mould (G_2) of dorsal valve. **H**. MGM 5896X, internal mould of ventral valve. **I**. MGM 5899X-1, internal mould of dorsal valve. **J**. MGM 5913X-1, internal mould of ventral valve. **K**. MGM 5899X-2, internal mould of dorsal valve. Scale bars 5 mm.

less flattened valves, especially on their posterocentral region, while they have a rounded section on the most flattened marginal areas. According to Havlíček and Branisa's (1980) description of *E. orthiformis* it differs from the Peruvian specimens by the absence of concentric lines and in displaying maximum width at the hinge line. Nevertheless,

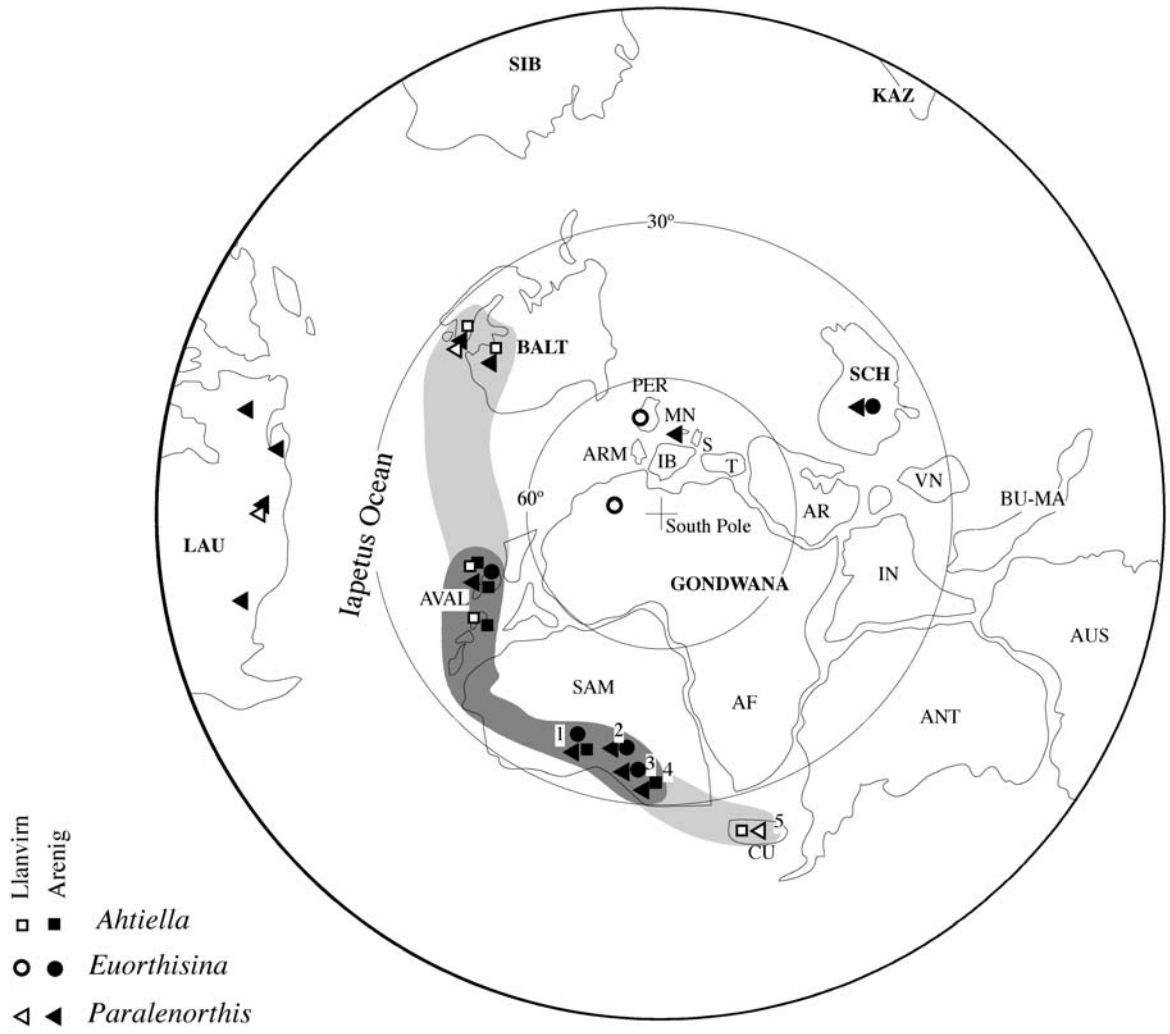


Fig. 8. Palaeogeographical reconstruction of the southern hemisphere for the Early-Mid Ordovician transition, based on Terra Mobilis (Scotese and Denham 1988), with the distribution of the studied brachiopod genera. Dark grey area indicates distribution of *Ahtiella* during Arenig times; light grey area indicates regions invaded by *Ahtiella* during Llanvirn times. Gondwana: AF, Africa; ANT, Antarctica; AR, Arabia; ARM, Armorica; AUS, Australia; AVAL, Proto-Avalonia; BALT, Baltica; BU-MA, Burma-Malaisia; CU, Cuyania (Precordillera); IB, Iberia; IN, India; KAZ, Kazakhstania; LAU, Laurentia; MN, Montagne Noire; PER, Perunica (Bohemia); S, Sardinia; SAM, South America (1, Peru; 2, Bolivia; 3, Eastern Cordillera Argentina; 4, Puna-Famatina); SCH, South China; SIB, Siberia; T, Turkey.

in Havlíček and Branisa's (1980: pl. 4: 12; pl. 5: 20) illustrations well preserved fila are seen, as well as the maximum width of shell well anterior to hinge line, as it occurs in the studied shells. Actually, an oval outline and a filate ornament are features very typical of the European species of *Euorthisina* and, in spite of Havlíček and Branisa's (1980) descriptions of the Bolivian *E. orthiformis* and *E. kobayashii*, they seem to be characteristic of them, too.

Palaeogeographical considerations

The Lower Ordovician brachiopods of South America display important differences between basins and are considered to represent distinct faunal provinces related to different palaeocontinents. Benedetto (1998a, 2003a) depicts a scenario describing three main faunas of biogeographic significant in Argentina: (1) The Precordilleran Faunas with mixed affinities with Laurentian, Celtic and Baltic faunas; (2) the Puna-Famatina Faunas with a Celtic signature, and (3) the Eastern Cordillera Faunas of Mediterranean affinities and closely related to those from Bolivia (Havlíček and Branisa 1980). This variability within relatively short distances has promoted debate, contrasting a model that suggests the Argentine Precordillera was an exotic terrane derived from Laurentia that docked with Gondwana by the Mid or Late Ordovician (Astini et al. 1995; Thomas et al. 2002; Benedetto 2003a) and a second model that supports the Gondwanan affinity of the Precordillera terrane since the Cambrian (Aceñolaza and Toselli 2000; Aceñolaza et al. 2002; Finney et al. 2005; Finney 2007).

The Early Ordovician brachiopods from the Andean Eastern Cordillera, described up to now from Bolivia (Havlíček

and Branisa 1980) and Northwestern Argentina (Benedetto 1998b; Benedetto and Carrasco 2002; Benedetto 2003b; Harper et al. 2004; Villas and Herrera 2004), display Mediterranean affinities and a close relationship with north Gondwana, as supported by the occurrence of species of *Euorthisina*, *Incorthis*, *Kvania*, and *Tarfaya*. Nevertheless, they also display certain connections with proto-Avalonian faunas, as suggested by the occurrences of *Astraborthis* and *Monorthis* genera (Benedetto 1998b; Benedetto and Carrasco 2002). The studied Ordovician outcrop of Peru is among the northernmost of the Central Andean Basin. The proximity of the Region to Bolivia during the Early Ordovician, must have been similar to the present day, allowing the exchange of common species such as *Paralenorthis immitatrix* and *Euorthisina orthiformis*.

The Peruvian brachiopod associations are of very low diversity, with only three recorded genera in total: *Ahtiella*, *Euorthisina*, and *Paralenorthis*. The last is cosmopolitan (see Fig. 8), with known occurrences from all palaeolatitudes and palaeocontinents (Jaanuson and Bassett 1993). *Euorthisina* was restricted to Gondwana and some peri-Gondwanan tectonic plates, being known from the mid to high-latitude northwest margin of Gondwana in Bolivia (Havlíček and Branisa 1980), north-west Argentina (Benedetto 1998b), Peru (this paper), Bohemia (Havlíček 1951) and Morocco (Havlíček 1971) with a further extension into the mid-latitude peri-Gondwana microcontinent of south-west China (Xu and Liu 1984; Zhan et al. 2006). All of them are Arenig in age, except the Bohemian and the Moroccan species that are both of Llanvirn age. *Euorthisina* is also known from the proto-Avalonian fragment of Shropshire in the Welsh Borderland (Williams 1974), Arenig in age in association with more typically Mediterranean than Celtic taxa.

The Celtic brachiopod assemblages (Neuman 1984) are known to be restricted palaeogeographically to the southern part of the Iapetus Ocean, with most of their records from islands and microcontinents associated with Avalonia (Harper et al. 1996). The Celtic Province was originally described by Williams (1973) as characterised by brachiopod assemblages from Anglesey (south Wales) and Tagoat (south-eastern Ireland). Actually, the faunal integrity of those brachiopod assemblages that characterise the Celtic Province is the main argument for considering Avalonia as a single terrane, placed at the margin of Gondwana during the Early Ordovician (Cocks and Torsvik 2002). Today it is dispersed in multiple fragments throughout North America and western Europe. *Ahtiella*, recorded herein from the Arenig of Peru, is frequent within the Celtic assemblages (Neuman 1984).

The two species of *Athtiella* described herein from the uppermost Lower Ordovician (Whitlandian, middle Arenig) represent the oldest record of the genus, besides the undetermined species from the Suri Formation figured by Benedetto (2003b: 210) in Famatina. Later, during the Mid Ordovician (Fennian, late Arenig), the genus migrated eastward from this region into the north margin of proto-Avalonia, being represented in Anglesey (South Wales; Bates 1968) as well as in Indian Bay and New World Island (Newfoundland; Neuman 1984). In the Llanvirn *Ahtiella* persisted within Avalonia (Central Newfoundland and Wales; Neuman 1984) and it also crossed the Törnquist Sea, reaching Baltica, where it is known from Sweden (Hessland 1949) and Estonia (Öpik 1932). During the early Llanvirn it migrated westward reaching the Precordillera Argentina region (Benedetto and Herrera 1986; Benedetto 2003b). This occurrence is consistent with the close proximity of the Precordillera (or Cuyania) to autochtonous Gondwanan platform by the Mid Ordovician, independent of its possible earlier palaeogeographical origin.

It is clear that, during the Arenig times, the Peruvian margin of Gondwana must have been very close to the autochthonous margin of the Avalonian continental fragments, before they drifted off from Gondwana. This idea is supported by the palaeogeographical restorations where proto-Avalonia is placed close to the north-western margin of South America in similar latitudes as the Eastern Cordillera, such as those by Cocks and MacKerrow (1993: fig. 1), Benedetto (1998a: fig. 6), Cocks and Torsvik (2002: fig. 1) and Murphy et al. (2006: fig. 17). Less probable are those configurations that move Avalonia away from South America, placing it close to the south-western Europe (Neuman and Harper 1992: fig. 3; Harper et al. 1996: fig. 4).

The latest ideas are incorporated into the palaeogeographical reconstruction for the Arenig of Fig. 8, based on that by Cocks and Torsvik (2002: fig. 1) although employing the more schematic palaeocontinent reconstructions of Terra Mobilis (Scotese and Denham, 1988). The main modifications to the restoration by Cocks and Torsvik (2002) lies in the situation of the Southwestern European Platform of Gondwana (with known remnants in Armorica, Iberia, Montagne Noire, Sardinia, and Bohemia-Perunica). The Southwestern European Platform is placed adjacent to Gulf of Libya, following Gutiérrez-Marco et al. (2002). Closer proximity of Avalonia with the Central Andean Basin in similar temperate latitudes, than with the Southwestern European Platform, placed in very high latitude, is justified by the brachiopod affinities. We have followed Aceñolaza et al. (2002), Finney et al. (2005) and Finney (2007) in placing the Cuyania (or Precordillera) terrane at the southern margin of West Gondwana (present coordinates).

Assuming the above palaeogeographical restoration, it can be concluded that *Ahtiella* was a genus restricted to temperate latitudes. It has never been recorded from sub-polar regions, such as those of North Gondwana, or palaeo-equatorial ones as those from Laurentia, Siberia or even those from East Gondwana. Its northernmost known excursion was into the Cuyania terrane during the Llanvirn, with well constrained latitudes slightly lower than 30° by the time. *Euorthisina* also spread during the Arenig throughout the middle latitude belt at the Gondwana margins, but it also colonised sub-polar latitudes, coinciding with the Llanvirn transgression over North Gondwana. The third recorded genus from Peru, *Paralenorthis*, had no latitudinal restrictions and was able to cross even the wide Iapetus Ocean.

The Avalonian connections of the Ordovician brachiopods and trilobites from Peru persisted during the Llanvirn, as shown by the assemblages described by Hughes et al. (1980) from the Contaya Formation of eastern Peru (*Tissintia simplex*, *Ogygiocarella* cf. *debuchii*, *Anebolithus tafuri*, *Porterfieldia contayaensis*)

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